Some black-and-white facts about the Faeroese white-speckled Common Raven *Corvus corax varius*

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Summary.—The white-speckled raven, a colour aberration of the Faroese Raven *Corvus corax varius* Brünnich, 1764, has occurred in the Faroe Islands since at least the Middle Ages. It has been described in many publications, and was a desired object for collectors of curiosities, especially in the 18th and 19th centuries. Early in the 20th century (1902) the last white-speckled individual was seen in the Faeroes, leaving only about two dozen specimens in museum collections. Although often referred to as albino, the aberration causing the white feathers is not albinism but leucism.

Common Raven *Corvus corax* Linnaeus, 1758, has a circumpolar distribution in the Northern Hemisphere. In addition to nominate *C. c. corax*, ten subspecies have been described, including the slightly larger *C. c. varius* Brünnich, 1764, which is endemic to the Faeroes and Iceland. The white-speckled variant of *C. c. varius* was known only from the Faeroes. Salomonsen (1934a) discussed whether white-speckled birds might also have occurred in Iceland, as claimed by Olaus Magnus (1555), but doubted this for several reasons. It is unknown when the mutation first arose, but Ole Worm already had two specimens in his Museum Wormianum in Copenhagen, both collected before 1650 (Worm 1655).

By 1767 Ascanius had written that the white-speckled variant was not a separate species but a variety of Common Raven. However, in later descriptions both Vieillot (1817) and Wagler (1827) referred to it as a distinct species, giving rise to an ongoing debate concerning its taxonomic status.

Salomonsen (1934) described the presumed inheritance of white-speckled plumage based on historical records of the colours of pairs and their offspring. His study suggested a recessive inheritance for the black-and-white pattern, which is a form of leucism (van Grouw 2012, 2013). Recessive genes can be inherited invisibly via many generations before two birds, both carrying the recessive gene, mate, making the white-speckled gene visible in their offspring. Therefore, if this was indeed a recessive gene, it is difficult to be sure whether it has been lost, through time, since the last white-speckled bird was seen, or whether it might still occur in some individuals.

A remarkable bird, occurring in small numbers in a remote place, will inevitably be targeted by collectors. Both live birds and mounted specimens of the white-speckled raven were sent to museums and collectors of curiosities throughout Europe from the 17th century, although many specimens were subsequently lost or destroyed. Only 26 specimens remain in museums (van Grouw & Bloch in press).

Based on the numerous reports in the literature, one can acquire a fairly good idea of the population size of the Faroese raven through time. It is obvious that it was very common until *c.*1850. Svabo (1783) mentioned 'large flocks', Landt (1800) stated that it was a well-known 'bird of prey', Graba (1830) saw many in 1828, and Atkinson (1989) said the same in 1833. Both Holm (1848) and Müller (1862) regarded the raven as common but Feilden (1872) saw fewer than expected. Annandale (1905) observed hardly any and, although the population

thereafter increased again, in 1930 Salomonsen (1931) still saw only small numbers, as did Ferdinand (1947) later. Bloch also observed few ravens in 1963, but in 1974 she noted a remarkable increase (Bloch *et al.* 2010). By 1981 at least 117 breeding pairs were counted on the Faeroes and the population was estimated at 150–350 pairs (Bloch & Sørensen 1984: 59). The recovery was mainly due to food supplies at waste sites of fish factories and incineration plants (Bloch 1981, Bloch & Sørensen 1984). Despite a legal requirement, introduced in 1988, for waste sites to be covered, limiting food for the ravens, the estimated number of breeding pairs in the Faeroes is currently *c.*500 (J.-K. Jensen pers. comm.).

The sharp decline in numbers on the Faeroes after 1850 was mainly due to the increase in the islands' human population, combined with the local beak tax still in force (Bloch 2012). The Faeroese National Archive contains lists from all six districts, covering most of the period 1742–1934, during which the annual number of ravens destroyed appears to have been *c.*150–250 (Bloch 2012). Around 1900 the population apparently reached its lowest ebb and the white-speckled variant became extinct.

The white-speckled mutation

Although the terms albino and partial albino are frequently used for the white-speckled ravens (Hartert & Kleinschmidt 1901, Sage 1962), the mutation causing the black-and-white pattern is a form of leucism. Leucism, from the Greek *Leukos* = white, can be defined as the partial or total lack of melanin in feathers (and skin) (van Grouw 2012, 2013). The lack of melanin is due to the congenital and heritable absence of pigment cells from some or all of those skin areas where they would normally provide the growing feather with colour. Depending on the type of leucism, the amount of white can vary from just a few feathers (= partial leucistic) to all-white individuals, which always possess colourless skin as well. Partially leucistic birds can have a normal-coloured bill and legs depending on where the colourless patches occur. However, leucistic birds always have pigmented eyes. To properly understand the nature of leucism it is necessary to know something of feather pigmentation first.

Melanins are the commonest pigments in birds and play a major role in the coloration of feathers, skin and eyes. They comprise two main types: eumelanin and phaeomelanin, which differ in colour, chemical composition and pigment granule structure (Fox & Vevers 1960). Eumelanin produces black, grey and brown feathers, and eye and skin colour, while phaeomelanin only occurs in feathers, and determines colours from deep reddish brown to pale buff. In all *Corvus* species only eumelanin is present, but for convenience it will simply be referred to as melanin hereafter.

Melanin is produced by specialised cells in the skin referred to as melanin cells or melanocytes, which develop from melanoblasts formed in the 'neural crest'—the embryonic spinal cord. Normally, melanoblasts migrate at an early embryonic stage to the mesodermal layers of the skin. Finally incorporated in the skin and feather follicles, melanoblasts develop into melanocytes to provide the feather cells with melanin (Crawford 1990).

The migration process is genetically determined and any (inheritable) change can affect the final distribution of the melanoblasts. If, due to a mutation, the melanoblasts are unable to migrate from the neural crest to the skin, there will be no melanocytes present to produce melanin, resulting in a completely un-pigmented (white) bird with pink skin. However, the eyes are not red (the crucial difference from albinos). The embryonic origin of eye pigments partially differs from that of the rest of the body; eye pigments are formed mainly from the outer layer of the optic cup (Lamoreux *et al.* 2010) and as leucism affects only the migration of melanoblasts originating from the neural tube it has no influence on eye pigmentation with an optic cup origin.

In addition to being all white, leucistic birds can be partially white, with colourless feathers adjacent to normal ones. The pied appearance can be caused by a delay in the migration of the melanoblasts from the neural tube to the skin (Wagener 1959, Wendt-Wagener 1961). Because of the delay, some melanoblasts reach certain parts of the body where the skin is too far developed to incorporate them, resulting in these parts lacking colour. Another possibility is that, from the outset, insufficient melanoblasts develop in the neural crest and therefore not all parts of the body are provided with pigment cells (Daneel & Schumann 1961, 1963).

The white in leucistic birds is often patchy and bilaterally symmetrical due to the way melanoblasts migrate to the rest of the body, leaving certain areas without pigmentation. The white pattern is already present in juvenile plumage and the amount of white does not change with age. The commonest form of leucism affects pigment in body parts furthest from the neural crest: the face, the 'hand' of the wings, the feet and belly. This form caused the white-speckled plumage of Faroese ravens.

Although this form of leucism is commonest and occurs in many bird species (Fig. 4), leucism in general is uncommon. A far more widespread cause for the lack of pigment in feathers is progressive greying (van Grouw 2012, 2013) but this is not discussed further here.

Presumed inheritance and leucism in related species

The black-and-white pattern in ravens was uniform and symmetrical, following the pattern of the commonest form of leucism in birds; absence of pigment in the body parts furthest from the pigment cells' origin (Figs. 1–2). The total area of affected skin parts may differ, with smaller or larger white patches as a result, but generally the head and throat are white, as are the belly, primaries and primary-coverts, and claws. In extreme cases almost the entire wings are white, and the white throat extends to the belly breaking the black pectoral band.

Depending on where in the face pigment is lacking, the melanins in the eyes may be absent too, resulting in only those pigments that formed in the optic cup being visible. These appear to be much paler as, according to Graba (1830), who examined two freshly shot white-speckled ravens, the eyes were grey greenish-white ('*Iris graugrünlichweiss*'). In other species, e.g. Rook *Corvus frugilegus* and Greylag Goose *Anser anser*, bluish-white eyes occur in leucistic individuals.

Different genes in birds result in this leucistic pattern. In Mallard *Anas platyrhynchos* it is due to a dominant gene, while in Japanese Quail *Coturnix japonica* it is recessive. It is partially dominant in Helmeted Guineafowl *Numida meleagris*: if the gene is present just once (heterozygous) the bird will possess the white pattern, while the presence of two genes (homozygous) produces an all-white bird. The same is true in Zebra Finch *Poephila guttata* (Fig. 3), although in this case another recessive gene is the cause.

Nothing is known with certainty concerning inheritance in genus *Corvus*. It has not been recorded in ravens except in the Faeroes (van Grouw 2012). Nor is it known to have occurred in Carrion Crow *Corvus corone*, but *is* found very rarely in Hooded Crow *C. cornix* and Jackdaw *C. monedula*. In Rook, however, it is reasonably frequent, though in some cases only a small patch of white feathers is present on the chin, occasionally with 1–2 white claws. Given that Rooks lose most of their facial feathering on reaching adulthood, leucism is probably under-recorded. A juvenile leucistic Rook was described as a separate species by Sparrman (1786), who named it *Corvus clericus* (Latin for priest) on account of its white 'bib' (Fig. 8). There is, however, considerable variation in the white chin's size and, the larger it is, the more likely it is to be accompanied by white primaries and claws. More extreme

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Figure 1. Drawing of a life-like white-speckled Common Raven *Corvus corax* in flight (Katrina van Grouw)

Figure 2. White-speckled Common Raven *Corvus corax* specimen in the Überseemuseum Bremen, Germany (UMB 3800), collector and collection date unknown, but probably pre-1870 (Gabriele Warnke)

cases follow the same pattern as in Common Raven (Fig. 5).

According to Salomonsen (1934) the inheritance of leucism in Common Raven was recessive, based on different crossings mentioned in the literature: two black parents may produce white-speckled offspring (Ascanius 1767, Graba 1830, Holm 1848, Müller 1862) and a white-speckled crossed with black may also yield white-speckled young (Graba 1830, Holm 1848, Müller 1862). In all cases white-speckled ravens hatched only when black parents were heterozygous (= carrying the allele for white-speckled once). Unfortunately, no records are available of crossings between two white-speckled birds. Based on these pairings, provided they are correct, straightforward recessive inheritance for white-speckled appears to be true. However, that this genetic variety was lost during the period that the variants were hunted to extinction, *c.*110 years ago, is in contrast to the recessive trait. Many black ravens in the Faeroes must have been heterozygous for leucism and the gene would be carried for many generations after the last white-speckled bird was seen. Sooner or later two heterozygous individuals would presumably have paired, producing white-speckled offspring. However, during the last century no pied ravens have been reported, but this might be explained by the severe decline in the population as a whole in the second half of the 19th century.

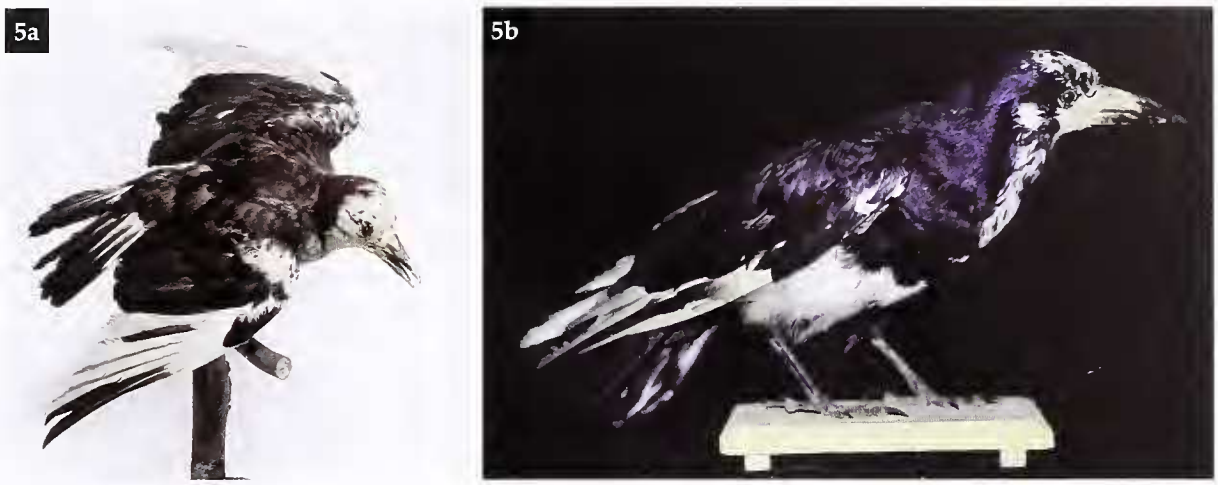

Figure 3. Comparable leucism in different bird species: above, Bengalese finch *Lonchura domestica*; bottom, Zebra Finch *Poephila guttata* (Pieter van den Hooven)

Figure 4. Comparable leucism in different bird species: Common Moorhen *Gallinula chloropus*, Durham, UK, January 2010 (Glen Roberts)

Figure 5. Leucistic Rooks *Corvus frugilegus*: left, juvenile, State Darwin Museum Moscow (SDM OF61) (Igor Fadeev); right, adult, formerly at Zoological Museum Amsterdam (ZMA 54604, now at NBC Naturalis) (Hein van Grouw)

As there are no reliable estimates of the proportions of white-speckled ravens and black ones, it is impossible to calculate the presumed gene frequency in a specified timeframe. However, with some assumptions we can acquire an impression of how common the allele for white-speckled could have been. Given that ravens were still common in the mid 1800s (Holm 1848, Müller 1862), we might assume that the pre-1850 population comprised *c.*120 breeding pairs (240 individuals). White-speckled individuals were not uncommon then (Graba 1830), so let us assume they comprised 10% of the population (24 birds). Of the 216 black birds a percentage were heterozygous. Knowing that the mutation had been present for centuries and that white-speckled individuals were breeding, it is plausible that 50% carried the allele for white-speckled (108 birds). Symbolising black as A and white-speckled as a, the number of genotypes in the population were: 108 AA, 108Aa and 24 aa, i.e. 45% did not carry the white-speckled gene (AA), 45% were carriers (Aa) and 10% were white-speckled (aa), thus the white-speckled gene was present in 55% of the raven population.

If we consider all white-speckled individuals eliminated, the a-allele in single form is still present in 50% of the population; that is, 108 pairs of black ravens (216 individuals; 108 AA and 108 Aa). In this scenario, four different crosses are possible and all equally probable (AA × AA = 100% AA; AA × Aa = 50% AA and 50% Aa; Aa × AA = 50% AA and 50% Aa; Aa × Aa = 25% AA, 50% Aa and 25% aa). Expressed as a percentage, the genotype of the offspring of these 108 pairs is: 56.25% black and lacking the gene for white-speckled (AA); 37.5% black and carrying the gene for white-speckled (Aa) and 6.25% white-speckled (aa). By removing the white-speckled individuals, a-gene frequency will be reduced, but if the population is sufficiently large the gene will still be present. However, the natural process of genetic drift can cause loss of certain alleles, especially in small populations.

Genetic drift is the random change in allele frequency in a population and is, along with selection, mutation and migration, a basic mechanism of evolution. These mechanisms cause changes in genotypes and phenotypes over time, and determine the degree of genetic variation within a population. In a textbook scenario, the alleles in the offspring form a representative sample of those in parents. However, in practice, certain alleles may be unrepresented in the next generation, especially if the number of offspring is low.

Figure 6. Diluted Common Raven *Corvus corax*, Velbastaður, 2 March 2008 (Hans Eli Sivertsen)

Figure 7. Diluted Common Raven *Corvus corax* specimen shot at Fugloy in 2008, prepared by J.-K. Jensen and donated to the Museum of Natural History, Tórshavn (Jens-Kjeld Jensen)

Figure 8. *Corvus clericus*, described by Sparrman in 1786 in *Museum Carlsonianum*, was in fact a leucistic Rook *C. frugilegus* (Harry Taylor / © Natural History Museum)

These alleles are therefore lost to subsequent generations.

The degree of loss of genetic variation (dF) is inversely proportional to the number of breeding individuals (N). The following formula illustrates the correlation between dF and N: $dF = {}^{1}/_{(2N)}$ (Ouborg 1988). This shows that the loss of alleles is higher in proportion to the number of breeding birds. Moreover, in small populations genetic variation decreases more rapidly. Besides that white-speckled individuals were hunted because of their value to collectors, the beak tax caused an overall decline in the raven population. In all, it is plausible that the allele for

white-speckled was recessive and was lost when the raven population reached its lowest abundance.

Last observations of white-speckled ravens

Records in the literature always referred to white-speckled or pied ravens, which were known to the Faroese people by the name Hvitravnur. Occasionally 'white' specimens may have been reported, as Debes (1673) suggested, but he also stated that 'the white ravens are not entirely white, but speckled with black feathers'. Because of their curiosity, white speckled-ravens were always highly prized. In the latter half of the 19th century especially, when the raven population was suffering intense persecution, white-speckled birds were even more severely hunted, leading to their extinction in the early 20th century. Several observations of presumed white-speckled birds were made post-1900: (1) 2 November 1902, Mykines (Andersen 1905, Salomonsen 1934), (2) autumn 1916, Velbastaður and Koltur (Ryggi 1951), (3) winter 1947 and again in late 1948, Nólsoy (Ryggi 1951), and (4) before Easter 1965, Sandvík (Nolsøe & Jespersen 2004).

In winter 1988/89, a 'white' raven was seen around Tórshavn (J.-K. Jensen pers. comm.) and again at Velbastaður throughout winter 2007/08. It was photographed on 2 March 2008 (Fig. 6), clearly revealing that it was not a white-speckled individual. In this case, and almost certainly in three of the four cases listed above, a different mutation was involved, namely dilution. Dilution is a quantitative reduction of melanins (van Grouw 2013) meaning that the number of pigment granules is reduced, but the pigment itself is unchanged. Therefore, due to the lower concentration of granules than normal, a 'weaker' or 'diluted' colour occurs. This can be compared to a photograph in a newspaper; a high concentration of black ink dots close together is perceived as black, while fewer black dots in the same-sized area appear grey. Dilution is not uncommon in Carrion Crow, Hooded Crow and Rook.

The bird at Velbastaður was last seen in April 2008, and this, or another diluted individual, later in 2008 at Suðuroy. Earlier the same year another was shot at Fugloy and donated to the Museum of Natural History in Tórshavn (Fig. 7). Additionally, in August 2008, one was at Viðareiði and two more at Fugloy. In December 2009 another was seen twice at the south end of Suðuroy. All those seen in 2007–09 appeared to be young (J.-K. Jensen pers. comm.). Their fate is unknown.

Obviously, the gene for dilution is present in Faroese ravens and probably has been for a considerable period. Returning to the observations in 1916, 1947, 1948 and 1965, all of these records were listed as 'white' ravens and not 'white-speckled'. Given that the gene for dilution is present and this aberration causes a solid grey-white plumage coloration, it is probable that these records were all diluted individuals. Only the record of 1902 mentioned white-speckling and therefore this date is considered the official date of extinction of the white-speckled variant of the Faeroes raven.

Conclusion

Despite being an icon for several centuries, the last white-speckled Faeroes raven was shot in 1902. One can assume that, along with the bird, the recessive allele for white-speckled plumage was also lost as a result of genetic drift combined with the severely depleted population. In addition to the species being hunted for pest control purposes, especially in the 19th century, white-speckled birds were consistently targeted by bird collectors.

The white-speckled plumage was caused by a recessive gene mutation known as leucism: a lack of melanin pigment due to the congenital and heritable lack of pigment cells from some or all of the skin parts where they would normally provide the growing feather

with pigment. Inheritable leucism in birds is rare, but the black-and-white pattern in ravens (lack of pigment in the face, the 'hand' of the wings, the feet and belly) is the commonest form and occurs in many bird species.

Although the allele for leucism is apparently lost, another inheritable, recessive colour mutation now occurs in Faeroes ravens; dilution—a quantitative reduction of melanin pigment that produces a solid silvery grey plumage. Dilution is less rare and is occasionally found in other raven populations in North America and Europe.

To date, there are no confirmed records of diluted ravens breeding in the Faeroes, or elsewhere, but there is no reason to suppose that is impossible. Therefore, given that the Faeroe ravens represent an island population, the allele for dilution may become established in the future, just as the allele for leucism was in the past. Other island species offer examples of inheritable colour aberrations in their populations, of which the best is probably the flightless Weka *Gallirallus australis* in New Zealand. Three independent inheritable colour aberrations, melanism, leucism and progressive greying, occur in the South Island population (pers. obs.), and the extinct White Gallinule *Porphyrio albus* of Lord Howe Island was the result of inherited progressive greying in the local Purple Gallinule *P. porphyrio* population (Hume & van Grouw submitted).

For at least a century, carriers of the dilution allele have been present on the Faeroes and a new icon in the island's avifauna is likely to arise, albeit only if diluted individuals are not targeted as a collector's item. The continued occurrence of 'white' ravens on the Faeroes is conditional upon naturalists of the future learning a lesson from the past.

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